

# CODING OF SPATIAL POSITION IN THE SUPERIOR TEMPORAL SULCUS OF THE MACAQUE

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**Abstract:** The cortex of the anterior superior temporal sulcus (STSa) contains cells responsive to biologically significant stimuli such as faces and bodies. Anatomical studies suggest this region is a site for the integration of form and position information, yet few STSa cells have been demonstrated to be spatially sensitive. In the current study the activity of STSa cells was recorded in response to stimuli presented at different positions around the testing room. Evidence for spatial sensitivity was observed for 39 cells responding transiently to the sight of the experimenter (static or moving). The majority of these (36) showed selectivity for the distance of the stimulus from the subject. For a smaller number of cells, selectivity for lateral position was found. These preliminary results suggest that high level visual areas within the ventral stream of processing which is assumed to underlie object recognition (specifying "what" stimuli are) may additionally be influenced by "where" stimuli occur in space.

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## INTRODUCTION

### Dorsal and ventral streams of cortical visual processing

Primarily on the basis of lesion studies of primates, Ungerleider and Mishkin (1982) proposed the separation of visual processing into two separate cortical streams, one processing object position (dorsal parietal stream) and the other object recognition (ventral temporal stream). Such a division of the visual system has been supported by anatomical studies in non-human primates (e.g. Baizer et al., 1991; Morel & Bullier, 1990; Young, 1992) and by neuropsychological (e.g. Milner & Goodale, 1995) and functional imaging studies in humans (e.g. Haxby et al., 1991; Köhler et al., 1995).

At the neuronal level, cells in inferior temporal cortex respond selectively to complex visual stimuli. The cells also show stimulus invariance in that they maintain this selectivity over changes in stimulus size (e.g. Ito et al., 1995), partial occlusion (Kovács et al., 1995), defining cue (e.g. luminance, texture or relative motion – Sáry et al., 1993) and retinal position (e.g. Lueschow et al., 1994; Ito et al., 1995). These properties suggest coding for abstract stimulus shapes and are entirely consistent with a role of temporal cortex in object recognition.

Early physiological studies of the dorsal stream showed cells with contrasting properties. In parietal cortex, cells showed visual responses related to reaching and grasping (e.g. Mountcastle et al., 1975), motion perception and eye movements (Andersen, 1989). The sensitivity of each class of cells to object position and distance is consistent with the proposed spatial functions of the dorsal stream.

The division of function between dorsal and ventral streams proposed by Ungerleider and Mishkin (1982) has often been termed “what” versus “where”. An alternative view, advanced by Milner and Goodale (1995), suggests that “what” versus “how” is a more appropriate dichotomy. Focusing on the outputs of the system rather than the inputs, they emphasised the visuomotor nature of processing within parietal areas. Thus, the two visual pathways can be seen as subserving object or scene recognition and visuomotor behaviour, respectively. One implication of this model is that *form and space* may be processed in *both* pathways but for different functions. For example, information about form is required for both identifying and picking up an object. Indeed, studies suggest that some aspects of form are processed in the dorsal stream (e.g. Goodale et al., 1991) and reciprocally some aspects of space (e.g. distance) are processed in the early parts of the ventral stream (e.g. Dobbins et al., 1998).

At the neuronal level, cells with responses during hand actions in parietal cortex have been found to code the size and orientation of objects (Taira et al., 1990; Sakata et al., 1998; Murata et al., 1996). Such neurones may be involved in matching prehensile hand movements to the spatial characteristics of objects. Furthermore, Sereno and Maunsell (1998) found selectivity for 2-D shapes in the responses of neurones in the lateral intraparietal area of macaques in a fixation task. Such selectivity is equivalent to the shape selectivity observed in areas of the ventral pathway (e.g. inferotemporal cortex). This shape selectivity was observed in parietal cortex even though the subjects were not required to manipulate or grasp objects and may be related to intentional or attentional shifts.

In the ventral stream, Dobbins et al. (1998) reported distance-dependent changes in neural response to visual stimuli in area V4 of the macaque. For many cells, such effects were independent of retinal image size. Since V4 lies at an intermediate level in the ventral visual pathway, one might expect coding of distance to continue into temporal cortex.

Thus, recent neurophysiological studies support the claim for form and spatial sensitivity in both dorsal and ventral cortical visual streams. Such neurophysiological evidence is consistent with the Milner and Goodale model of cortical visual processing.

### Superior temporal sulcus

Cells within STSa of the macaque have been found to respond to biologically significant stimuli such as faces and bodies, and their motion (e.g. walking; Perrett et al., 1989, 1991). In particular, cells have been found responsive to facial expression and gaze direction and STSa has been proposed to play a critical role in social cognition (e.g. Emery & Perrett, 1994).

The status of the superior temporal sulcus with regard to the two cortical visual streams is not entirely clear. The posterior portions of the sulcus (in particular the motion sensitive areas MT, MST and FST) are associated with the dorsal stream, but the more anterior portions in the temporal lobe have been considered part of the ventral stream. Certainly the presence of cells sensitive to complex patterns in STSa are consistent with the putative role of the ventral stream in object recognition.

Anatomical studies have implicated STSa as a potential site for the integration of spatial, motion and object information (Boussaoud et al., 1990; Morel & Bullier, 1990; Baizer et al., 1991; Young, 1992). Indeed a convergence of projections from the posterior parietal cortex and inferior temporal cortex takes



place in the floor of STSa but not elsewhere amongst the posterior visual areas (Baizer et al., 1991). Physiological studies confirm the convergence of information about the motion and form of objects within STSa at the cellular level (e.g. Oram and Perrett, 1996) but, as yet, there is little evidence for spatial coding within STSa.

## Frames of reference in visual coding

Viewer-centred descriptions of objects define the position, movement and orientation of object components with respect to the viewer. Such descriptions may also be termed egocentric and are essential for guiding interactions with objects. By contrast, object-centred representations (envisaged by Marr and Nishihara, 1978) reference object components and their movement to a framework based on the object itself. An object-centred representation is therefore independent of the viewer's position and may also be termed allocentric (i.e. based on a framework centred on aspects of the environment rather than the observer). It provides an economical code for recognising an object or action.

Accounts of the two cortical streams of processing note that the viewer-centred sensitivity of cells (to object position and orientation) in the dorsal stream fits with their supposed visuomotor function. In the ventral stream one might expect object-centred coding to underlie the proposed recognition function. Relatively few cells, however, show the generalisation across viewing conditions that is characteristic of object-centred coding (Perrett et al., 1991). The majority of STSa cells selective for faces are sensitive to perspective view, orientation and image size (Ashbridge & Perrett, 1998). Such cell selectivity could be used to specify the orientation of a face relative to the viewer or other objects in the environment. In this way viewer-centred coding may be important for recognition. Theoretical accounts tend to overlook the importance of vantage point and relative spatial position for object and scene recognition. Biederman (1982) found that objects were recognised more slowly in real world scenes when the objects were presented at inappropriate positions (e.g. floating) than when the same objects were presented in normal relations to their setting.

A further type of allocentric coding (goal-centred coding) has been described for the responses of cells in STSa. Some of the cells selective for body movements are sensitive to the relative spatial positions of the agent performing the movement and the object or goal of the movement. For example, some cells responsive to the sight of reaching would fire only when the reaching movement brought the experimenter's hand to a particular location in space.

The experimenter's position could be varied so long as the final location of the hand was constant (Perrett et al., 1989).

Such an example illustrates the utility of combining coding of form with positional coding. Positional coding has only rarely been described in temporal cortex and has never been systematically studied.

## Size and distance

As distance increases, size of the retinal image decreases and vice versa. Studies of the effect of retinal image size on responses of neurones in the temporal cortex have produced conflicting interpretations. Most studies emphasise the finding that shape selectivity of cells is maintained across changes in the size of stimuli (e.g. Ito et al., 1995; Lueschow et al., 1994; Rolls & Baylis, 1986). It is apparent in all reports, however, that absolute size of stimuli does affect response magnitude.

Rolls and Baylis (1986) reported a trade-off between distance and retinal size for cells responsive to 2-D faces in STS. Thus, increasing the stimulus size could compensate for a reduction in cell response at an increased testing distance. In V1, however, a proportion of neurones is affected by viewing distance even if the retinal size is kept constant (Trotter et al., 1996) and sensitivity to distance independent of size was recently also observed in V4 (Dobbins et al., 1998) and may be maintained in higher visual areas such as STSa.

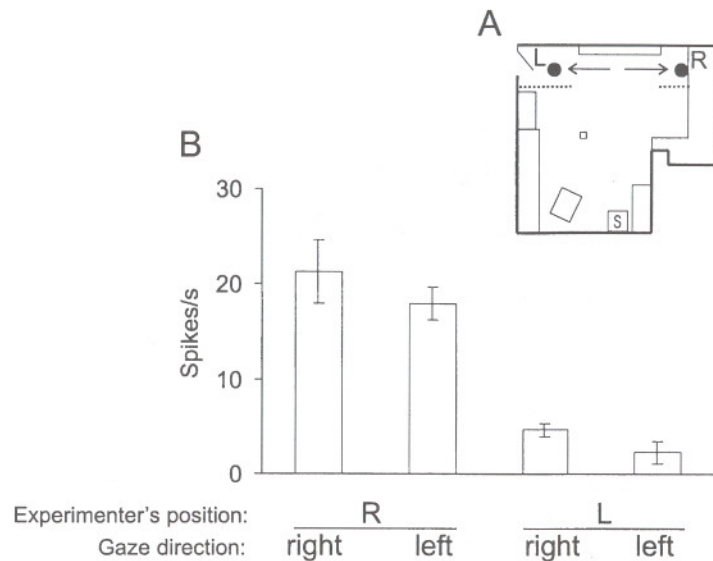
Ashbridge and Perrett (1998) reported that the majority of cells tuned to face and body views was sensitive to the size of whole body images projected at a distance of 4.0 m. Furthermore, the majority of cells was most responsive to life-sized images and showed decreased responses to images 1/4 to 1/2 life-size. For real, familiar objects of expected dimensions, retinal image size and distance are not independent and sensitivity to retinal image size should confer sensitivity to absolute distance. In the study of Ashbridge and Perrett (1998) however all testing was performed with 2-D stimuli at the same distance. Indeed, no study has examined the effect of distance on cell responses with familiar 3-D stimuli.

## Spatial sensitivity in STSa

We have recently studied a population of cells in STSa that code the presence of objects occluded from sight (Baker et al., in prep). All cells tested in this population (30/30) were found to be sensitive to the spatial position of the occluded



objects. This effect was found not to depend on eye position (see Fig. 1 based on Baker et al., in prep). This study has alerted us to the possibility of positional coding within the temporal cortex. Here, in this preliminary report, we examine the sensitivity of other classes of cells in STSa to the position of visual stimuli. We focus on cells selective for faces and bodies and ask whether the responses of these cells can signal the distance and lateral position of objects within the immediate environment of the observer.



**Figure 1** ♦ Spatial coding independent of gaze direction. **A.** Plan of test situation. S = subject position, filled circles show positions of experimenter during testing, dotted line = occluding curtains. The experimenter walked behind an occluding screen (arrows) situated either on the right (R) or the left (L) of the room. **B.** Histogram illustrating the mean ( $\pm 1$  S.E.) of the response of one cell recorded in STSa during the 1s period following occlusion. The cell responded more to occlusion of the experimenter at position R (right) than at position L (left). To investigate if this response difference was due to the position of the subject's eyes, we examined for each trial whether the monkey was looking to the right or the left of the room. For each stimulus condition 3 trials were selected where eye gaze was on one side of the room for the entire 1s period directly after occlusion. Overall, eye position had no significant effect (Mann-Whitney U,  $n_1 = n_2 = 6$ ,  $p > 0.42$ ). Eye position had no significant effect on the separate responses to the experimenter disappearing on the right (Mann-Whitney U,  $n_1 = n_2 = 3$ ,  $p > 0.37$ ) or the left (Mann-Whitney U,  $n_1 = n_2 = 3$ ,  $p > 0.18$ ). Overall, there was a significantly higher spike count after the experimenter disappeared on the right compared to the left (Mann-Whitney U,  $n_1 = n_2 = 6$ ,  $p < 0.004$ ). This indicates that the cell coded the position of the experimenter independently of gaze direction.

## METHODS

The subjects for these experiments were 2 male Rhesus macaques (*Macaca mulatta*): T (4 years old) and S (6 years old). Cell signals were recorded using standard electrophysiological techniques (e.g. Oram & Perrett, 1996). Any cells showing changes in firing rate during the presentation of various visual stimuli (including objects, the experimenter and slide and video images) were tested further.

Stimuli were presented through a liquid crystal shutter (aperture 20 by 20 cm at a distance of 15 cm) for controlled presentation, with a minimum of 5 trials per condition. Eye position during trials was monitored with an infrared camera mounted within a box containing the shutter. This monitoring allowed trials on which the subject failed to attend to the stimuli to be discarded from analysis. Stimuli (live, slide or video images) were presented in a pseudo-random order with each presentation lasting 1 second. Assessment of firing rates was based on a 500 ms period beginning 100 ms after the onset of the stimulus (corresponding to the average latency observed for cells in STSa – Oram and Perrett, 1996). Protocols were adapted to suit the selectivity of individual cells. Responses were analysed using between-subjects ANOVAs and Tukey post-hoc tests (level of significance  $p < 0.05$  throughout).

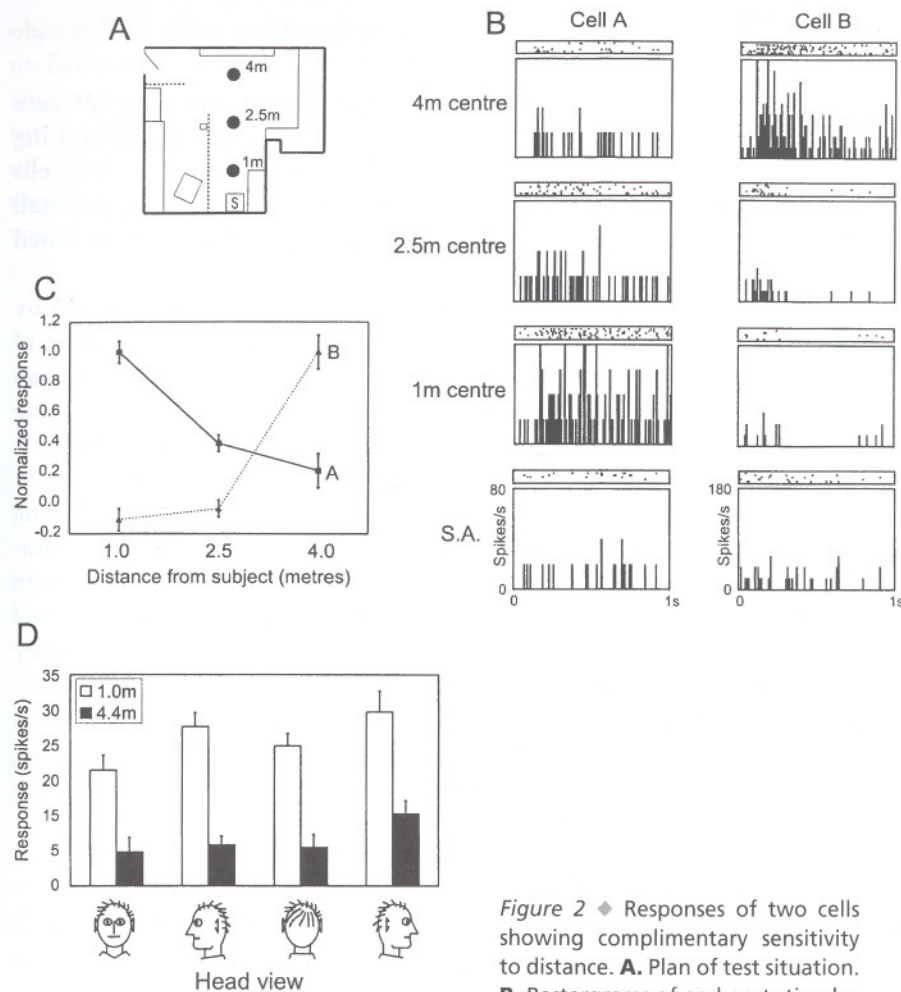
Testing for distance was always performed with real 3-D objects presented at distances ranging from 0.5 to 4.4 m and a range of lateral positions varying  $\pm 20$  degrees from straight-ahead (at the furthest distance of testing). Effects of lateral position were tested with both 3-D and 2-D images.

Cells were localised to the upper and lower banks of STSa (12-18 mm anterior to the inter-aural plane) on the basis of x-ray visualisation of microelectrodes. In one subject, recording sites were confirmed histologically with markers (DiI, Molecular Probes Europe BV; and micro-lesions) placed at the site of cell recording.

## RESULTS

Out of 463 cells with visual responses recorded in the anterior superior temporal sulcus, 69 (15 %) were observed to be sensitive to the position of stimulus presentation within the laboratory. This figure is likely to be an underestimate since the effect of position was not tested for all cells. The figure includes the thirty cells showing prolonged responses (up to 11 s) as an object moved out of sight that are described elsewhere (Baker et al., 1998, in prep). Here, we con-





**Figure 2** ♦ Responses of two cells showing complementary sensitivity to distance. **A.** Plan of test situation. **B.** Rastergrams of and post stimulus time histograms of the responses to

the sight of the experimenter at 3 distances of testing (1.0, 2.5, 4.0 m; see A) and a 'spontaneous activity' (S.A.) with no experimenter visible. **C.** Normalised mean ( $\pm 1$  S.E.) responses of the two cells as a function of viewing distance. Cell responses were normalised by expressing the cell response minus S.A. at a given test distance as a proportion of the maximum response minus S.A. The response of cell A decreases with testing distance ( $F(3,16) = 27.8$ ,  $p < 0.00001$ ). The response of cell B increases with test distance ( $F(3,16) = 34.7$ ,  $p < 0.00001$ ). **D.** Responses of cell A to different views of the head tested with 2-D stimuli (black bars) at 4.4 m and 3-D stimuli at 1.0 m (clear bars). Retinal image sizes of 2-D and 3-D stimuli were matched. 2-way ANOVA shows a main effect of condition ( $F(1,32) = 97.3$ ,  $p < 0.00001$ ) and a main effect of head view ( $F(3,32) = 4.0$ ,  $p < 0.02$ ) but no condition by view interaction ( $F(3,32) = 0.5$ ,  $p > 0.05$ ).

centrate on 39 cells that showed transient responses to the sight of the face or body. Twenty-one cells were responsive to static stimuli and 18 were selective for particular movements (e.g. arm movements). These cells are similar to STSa cells selectively responsive to faces and bodies reported previously (e.g. Perrett et al., 1989), in that the cells were not responsive to a variety of 2-D and 3-D control objects or their motion.

## Distance

The most prominent observation of positional sensitivity was that relating to distance of the stimulus from the subject. The responses of 36 cells were found to vary according to the distance of the visual stimulus from the subject. Note that all testing on the effect of distance was performed using the same experimenter (i.e. live 3-D) at all positions. For the majority of cells (35/36, 97 %) there was either an increase or a decrease in responsiveness with increasing distance of the stimulus from the subject (Fig. 2). For 25/36 (69 %) cells, responses were greater when the stimulus was close to the subject ( $< 2$  m) than when the stimulus was further away (2-4 m, e.g. Fig. 2, Cell A). For 10/36 (28 %) cells the opposite effect was observed with greater responses to stimuli presented further away ( $> 2$  m) than close ( $< 2$  m) to the subject (Fig. 2, Cell B). One cell presented with a live static human at 0.5 m, 1 m, and 3 m from the subject gave the greatest responses with the stimulus at the intermediate distance.

Distance effects, such as these, were observed both for cells responding to static faces and bodies and for cells selectively responding to particular body movements such as reaching with the arm.

## Retinal image size

The distance effects reported here could be interpreted as effects of retinal image size. For 5 cells tested, however, retinal image size alone did not determine distance sensitive responses to real faces. These cells showed greater responses to 3-D faces presented close to the subject than to 3-D faces presented far away and did not respond to the same degree to 2-D images of human faces of much larger absolute size, presented further away but subtending the same visual angle.

For example, cell A illustrated in Figure 2 showed greater responses to a real human head than to control 3-D objects of similar retinal image size. Responses were greater for real stimuli presented close to the subject than further away.



This cell was tested with different views of a real human head at a distance of 1.0 m from the subject, and with projected 2-D images of heads at a distance of 4.4 m (Fig. 2D). The visual angle subtended by the real human head and the projected images was maintained constant at 20 degrees. The cell also showed a degree of view selectivity, with the greatest responses to the right profile view of the head, for both real and projected images. For all views, the cell responses to the real face, close to the subject, were significantly greater than to the same head views projected at the same retinal image size at a distance of 4.4 m.

There are a number of variables that might account for these response differences. Some of these variables are related to distance (e.g. binocular disparity, angle of binocular convergence, overlap) and others are not (e.g. subtle changes in the nature of the face pattern). Furthermore an interaction between these variables may be important. This test, however, does indicate that the response change between near and far faces is not due to retinal image size alone, since retinal size is kept constant.

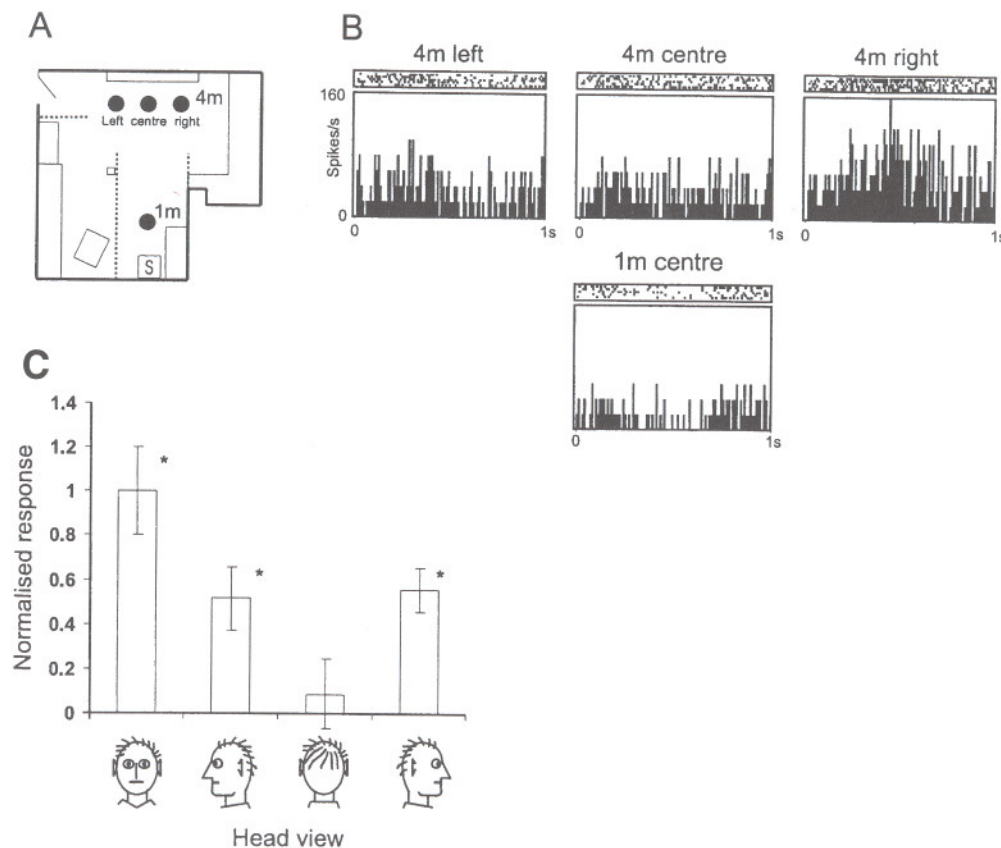
## Lateral position

Although distance effects were the most prominent positional effects observed, 4 cells were found with differential responses to identical stimuli presented at different lateral positions. As with the distance effects described above these differences were observed both for cells responsive to static and for cells responsive to moving stimuli.

For the cell illustrated in Figure 3 both lateral position and distance from the subject modulated the cell's response. This cell was tested with live static human stimuli at four different positions (4 m: left, right and central; and 1 m: central). Activity in response to the stimulus presented at all positions 4 m away from the subject was significantly greater than activity with the experimenter at 1 m from the subject. Thus there was an effect of the distance of the stimulus from the subject.

There was also a significant effect of the lateral position of the experimenter with the right position preferred to the central position and the left position. The cell seemed to be responding with a "hotspot" on the right side at the back of the laboratory. The cell was typical of STSa cells responsive to faces and bodies in showing view tuning (Perrett et al., 1991). The cell was tested in its preferred lateral location with different views of a static person. The front view elicited significantly greater responses than the back view (with the response to side views intermediate). This stimulus selectivity suggests that the coding of lateral position apparent in these cells is not explained by eye position alone:

while looking at the back, left and right profile and front views in the same location in the room, the eye position is the same, yet the responses are different. The fact that eye position is insufficient to explain the observed position sensitivity in STS is confirmed by the data from the study of a different STS cell class (Baker et al., 1998, in prep) shown in Figure 1.



**Figure 3** ♦ Sensitivity to distance and lateral position. **A.** Plan of test situation. **B.** Rastergrams and post stimulus time histograms of one cell's responses to the sight of the experimenter at different positions. Stimulus condition had a significant effect on response magnitude (ANOVA including an S.A. condition and 4 test positions,  $F(4,20) = 21.2$ ,  $p < 0.00001$ ). Tukey HSD post-hoc analysis revealed an effect of distance (with 4 m better than 1 m,  $p < 0.05$ ) and of lateral position (right larger than all other conditions, all  $p < 0.05$ ). **C.** Effect of stimulus view at the cell's preferred position (4 m right). Post-hoc analysis showed that the response to the front view was higher than that to all other views, and that the response to the back view was less than that to all other views. \* Represents activity significantly higher than S.A. ( $p < 0.05$ ).



## DISCUSSION

The results provide preliminary evidence for coding of spatial sensitivity at an anterior cortical site within the temporal lobe. This spatial sensitivity was found amongst cells that respond selectively to the sight of faces and other views of the head and body and their movements. The form sensitivity of such cells has previously been taken as evidence of the role of STSa in visual recognition of complex objects and actions. These results argue against a total separation of spatial and form information in the visual processing underlying recognition of objects and actions.

Visual processing of natural scenes underlying recognition of animate objects and their actions within the environment requires information on position. To interpret what an individual is attending to or interacting with, it is necessary to code a considerable number of visual cues (e.g. direction of gaze, head and body posture and motion). In addition, it is also necessary to code the positions of that individual and other objects in the environment. Egocentric analysis allows recognition of whether or not the individual is attending to or interacting with the observer (e.g. making eye contact). If attention is directed anywhere other than to the observer, then an allocentric framework of analysis is needed. The observer must specify the orientation and relative spatial positions of the individual and other objects to determine which object is the goal of attention.

These results confirm anatomical evidence suggesting that STSa is a site of integration of spatial and object information (Baizer et al., 1991). Anterior regions of the STS receive connections from parietal cortex (e.g. Baizer et al., 1991, Seltzer & Pandya, 1984), posterior regions of STS (including the motion areas MT, MST & FST - Boussaoud et al., 1990), parahippocampal cortex (Seltzer & Pandya, 1994) and entorhinal cortex (Good & Morrison, 1995). Any or all of these connections arising from areas outside the ventral stream could provide the spatial input to STSa that is required to account for the positional effects described here.

Dobbins et al. (1998) recently described distance sensitivity within the early stages in the ventral stream of cortical processing. A high proportion (> 60%) of cells in areas V1, V2 and V4 displayed changes in response with viewing distance. Area V4 forms the main visual input into inferior temporal (IT) cortex and STSa is one of the major output areas for projections from IT cortex. Position may therefore be coded throughout the ventral stream and the properties described here could be derived from processing within the ventral stream rather than the inputs from outside the ventral stream as described above.

## Visual cues for position coding

The present study indicates that position in depth and laterality affects cell responses in STSa to real faces and bodies. We have yet to define the visual cues that are utilised by the cells in deriving positional selectivity. Distance could be coded by cell sensitivity to retinal image size, although we have shown that the selectivity of some cells to distance cannot be accounted for solely by changes in retinal image size (cf. Rolls & Baylis, 1986).

For some of the cells, testing compared 3-D stimuli of one image size with 2-D images of equivalent retinal size but at an increased distance. Lack of response at an increased distance might reflect lack of response to 2-D stimuli, rather than a lack of response to the increased testing distance. Indeed, selectivity for 3-D stimuli has been reported amongst STSa cells responsive to faces (Perrett et al., 1984; Rolls & Baylis, 1986). The involvement of size cues might be disentangled by comparing 2-D stimuli matched in size but differing in distance (Dobbins et al., 1998). Of course, retinal image size and distance cannot be separated for most familiar objects with expected dimensions (one cannot present a real head at greater than life size at any distance). If cells show tuning for the form of familiar objects and are sensitive to retinal image size, then the cells will also be sensitive to distance. We have shown here that a substantial number of STSa cells tuned to the form of faces, bodies and their actions are indeed sensitive to distance from the observer over the range 0.5-4.4 m.

A small number of cells were found sensitive to lateral position. Again, it is not clear what cues this sensitivity might be based on. Obviously retinal image size is not a cue for lateral position. Since these cells were also selective for stimulus form at the preferred stimulus position (e.g. responding to one view of the body but not to a different view), the left-right positional sensitivity can not be explained by eye position alone.

Given the extensive viewer-centred coding in the ventral stream and prevalence of cells sensitive to view, orientation and size of faces in STSa, the spatial sensitivity of STSa cells might also be viewer-centred or egocentric. Such coding would depend critically on the position of the test stimuli relative to the observer. Moving the observer to a new position and leaving the test stimuli in the same position within the room should modify cell responses.

Recent accounts have speculated that the ventral stream may use an allocentric system of spatial coding in which the position of one visual stimulus is specified relative to the position of other visual stimuli or environmental cues (e.g. Dijkerman et al., 1998). Such allocentric coding could contribute to STSa cellular sensitivity to both lateral position and distance. If so, then coding should be relatively independent of the position of the viewer with respect to



the stimuli. Instead the coding should depend on the position of stimuli within the laboratory. In this case, moving the observer to a new position and leaving the test stimuli in the same position within the room should not modify cell responses. Such allocentric coding has been observed for STSa cells showing goal-centred responses (Perrett et al., 1989).

These alternatives are not mutually exclusive. Indeed, processing of position in the ventral stream could begin with an egocentric frame of reference and progress to an allocentric frame of reference. This might be achieved in much the same way that view-general (object-centred) cell properties can be generated by combining particular view-specific cell properties (Perrett et al., 1989).

## Lack of spatial sensitivity in previous studies

The question arises as to why previous studies have not observed the spatial sensitivity of cells in temporal cortex. Given the predominant view of function of the dorsal and ventral streams in cortical visual processing, most studies have concentrated on investigating object processing in the ventral stream neglecting possible effects of position. A similar bias has dominated research of the dorsal stream with studies concentrating on spatial perception but Sereno and Maunsell (1998) recently found parietal cells sensitive to visual form in fixation tasks.

The effect of retinal position of objects on the responses of cells in temporal cortex has previously been studied (e.g. Tovee et al., 1994). Such studies show that IT cells have large receptive fields with maximal responses in the foveal region. Such findings do not preclude additional modulation of cell responses according to position (in depth, laterality or height) of fixated objects particularly when object position is varied over large visual angles within a complex 3-D environment. We are not aware of studies that have investigated such effects in inferior temporal cortex. Should such studies be performed, they may well reveal coding of position similar to that seen in V4 (Dobbins et al., 1998) and STSa reported here.

## Acknowledgements

CIB was supported by St Leonard's College and the School of Psychology, University of St Andrews, CK by the Boehringer Ingelheim Fond and the Studienstiftung des deutschen Volkes, TJ by a Human Frontiers Science Programme and BW by MNERT (France).

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